

Notes on the biology, morphology, nomenclature and classification of *Pseudavga flavicoxa* Tobias, 1964 (Hymenoptera, Braconidae, Rhysipolinae), a genus and species new to Britain parasitizing *Bucculatrix thoracella* (Thunberg) (Lepidoptera, Bucculatricidae)

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Abstract

The solitary parasitoid *Pseudavga flavicoxa* has been reared, in some numbers, from cocoons of the bucculatricid moth *Bucculatrix thoracella* collected as larvae descending from *Tilia × vulgaris* to form their cocoons, at Jealott's Hill, Berkshire, England. The taxonomic confusions and complications bedevilling its determination are outlined, and the recognition of the genus *Pseudavga* Tobias, 1964 is proposed. Egg placement in this koinobiont ectoparasitoid and the related genus *Rhysipolis* is discussed.

Keywords

Cantharoctonus, *Rhysipolis*, *Pachystigmus*, France, Croatia

Introduction

Among parasitoids of Lepidoptera reared during 2010 and 2011 by IS and sent to MRS for determination was a small (2.2 mm) predominantly straw-orange female specimen of a cyclostome braconid of the subfamily Rhysipolinae. It had been reared, probably in spring 2011 [found dead], from a cocoon of the bucculatricid moth *Bucculatrix thoracella* (Thunberg) collected at Jealott's Hill, Berkshire, England on 13.ix.2010 as a larva descending from *Tilia × vulgaris* to spin up. The parasitoid was instantly recognised for what it was, as there are several similar specimens in the National Museums of Scotland (NMS) at the time provisionally standing over the incorrect name *Rhysipolis rustus* Papp, some of which were also reared from *Bucculatrix* in mainland Europe. However, no other British record or specimen had been seen, and nor had MRS been able to place them satisfactorily to genus within the tangled classification of Rhysipolinae. Further specimens reared from *B. thoracella* at Jealott's Hill have subsequently been obtained.

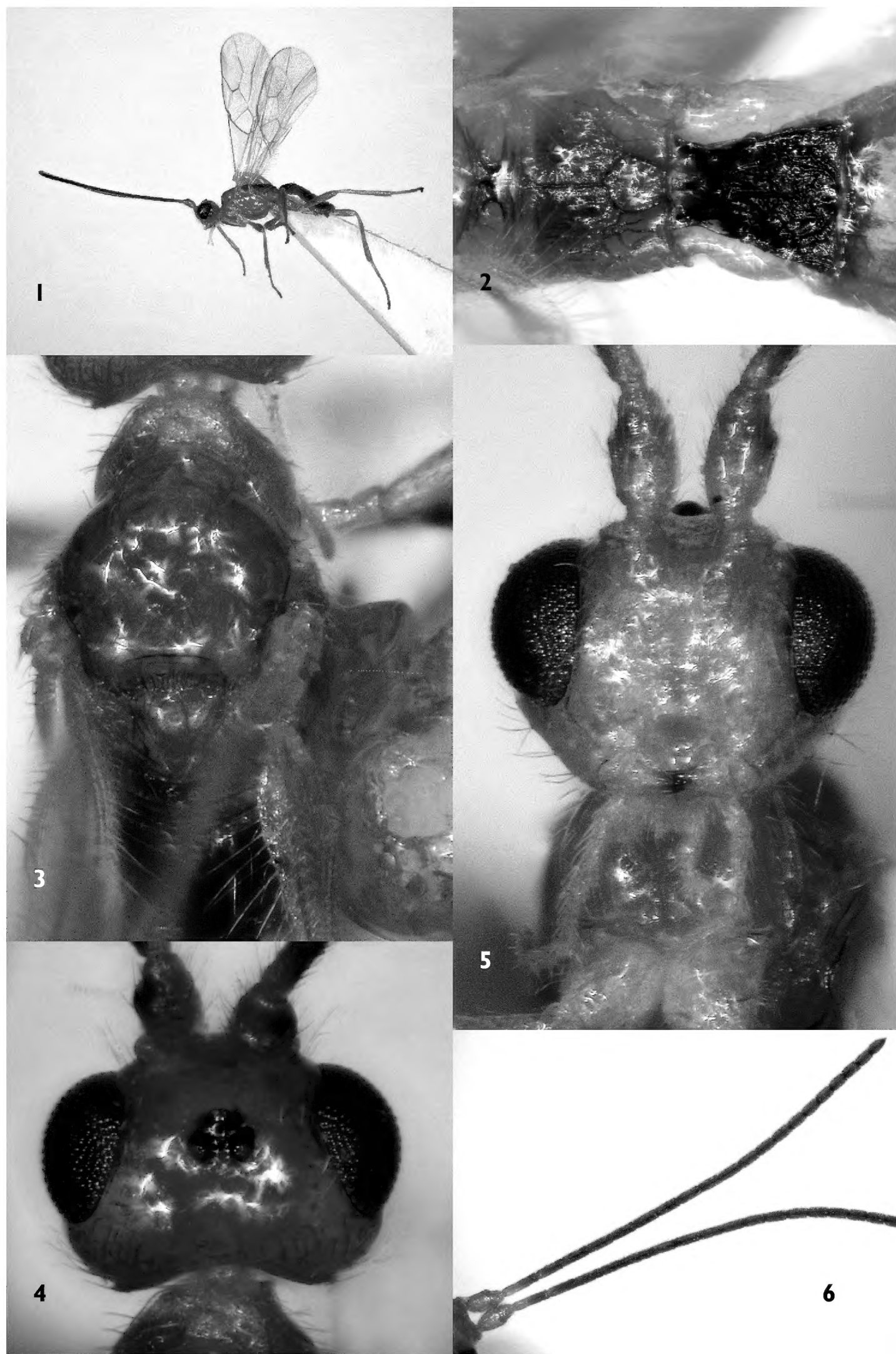
As well as simply bringing forth and figuring this species as a British insect (Figures 1–6), in this paper we review some of the taxonomic and nomenclatural morass surrounding its determination as *Pseudavga flavicoxa* Tobias, and propose the reinstatement of the generic name *Pseudavga* Tobias, 1964. In a work on Braconidae of the Russian Far East, Belokobylskij (1998) cites *Bucculatrix ulmella* Zeller (in fact from Moldavia) and (more surprisingly, in view of its different feeding habit) *Leucoptera malinifoliella* (Costa) as hosts of *flavicoxa* (as *Noserus*), but rearing records of *P. flavicoxa* in Western Europe have not previously been given.

In addition, some preliminary observations on the biology of *P. flavicoxa* are recorded, and both morphological and biological comparisons with *Rhysipolis* Foerster, 1862 are made. While the generic classification within Rhysipolinae remains in need of a wider review, morphological notes on the New World genus *Cantharoctonus* Viereck, 1912 are also given.

Materials and methods

All *B. thoracella* that produced *P. flavicoxa* were collected as descending larvae at Jealott's Hill, Berkshire, England (see “Biological observations” below). Experimental exposures involved wild *B. thoracella* larvae of various ages collected from *Tilia × vulgaris* in Edinburgh.

Figures 1–6 were made using a Leica MZ16 microscope and phototube with an Olympus C-5060 camera, with multiple images stacked using ZereneStacker. Figures 7, 8 and 10–13 were taken as single images on a hand-held Canon Powershot S110 directly down one arm of a Wild M5A stereomicroscope, and Figure 9 was taken with a Fuji Finepix S and Brunel SP100 trinocular microscope. Figure 14 was originally obtained on colour transparency film using a Contaflex camera and close-up lenses, with other details not recalled, and scanned.



Figures 1–6. *Pseudavga flavicoxa*, female. **1** habitus, lateral **2** propodeum and 1st metasomal tergite, dorsal **3** mesosoma, dorsal **4** head, dorsal **5** face **6** antennae.

Reared British material in NMS

Following the rearing of a single ♀ from *B. thoracella* collected in 2011 (see above), IS attempted to rear further specimens from this host from the same *Tilia × vulgaris* trees in the autumn of 2012, collecting around 150 host larvae. However, owing to a communication failure, only approximately half-grown larvae were collected, and only moths resulted. The following year, from 4.ix–19.x.2013, 92 fully grown descending larvae produced 2 ♀, 1 ♂ of *P. flavicoxa* in x. 2013, and a further ♀ was found dead by iv.2014; otherwise practically all cocoons produced moths in 2014. In autumn 2014, in preparation for more detailed research on the biology of the parasitoid proposed for 2015, a large number of descending larvae were collected from the same *Tilia* trees in the period 9.ix–4.x.2014, and the resulting cocoons were kept indoors until being dispatched to Edinburgh, where they were received on 10.x.2014. By that date around 20 *P. flavicoxa* (both sexes equally) had emerged from the earliest made collections (9–10.ix.2014), but the remaining *Bucculatrix* cocoons were immediately placed in an outdoor rearing shed (cf. Shaw 1997) and, apart from 1 ♂ on 16.x.2014 from the same early collections, no further emergences occurred (by 23.xii.2014): it is of course unclear whether or not more will emerge in 2015, but it is presumed that they will as the behaviour of the living adult females did not suggest preparation for hibernation. The range of antennal segments in the British material seen so far is ♀ 22–24; ♂ 24–26.

Continental material in NMS

Additional specimens, clearly congeneric with the British material and some reared from a further two species of *Bucculatrix*, are in NMS as follows:

CROATIA: 1 ♂, Oputija, ex *Bucculatrix frangutella* (Goeze), final instar larva coll. x.1988, em. x/xi.1988 (J.L. Gregory).

FRANCE: 1 ♀, Côte d'Or, Abbey de la Bussière, at light 21.vii.2003 (M.R. Shaw); 1 ♀, 1 ♂, Dordogne, La Barrière, 15 km S Ribérac, at light 4–12.viii.2007 (M.R. Shaw); and 1 ♀, same data but ex *Bucculatrix ulmella* on *Quercus*, coll. and em. viii.2007 (M.R. Shaw).

Results

Identity and nomenclature

A specimen from France present in NMS that is very similar to (certainly congeneric and provisionally regarded as conspecific with) the British reared specimens had been determined by MRS in 2003 as the nominal taxon *Rhysipolis rustus* Papp, based on the original description (Papp 1991). However by then Papp (2002) had placed his species in synonymy with what he referred to as *Noserus flavicoxa* (Tobias), the generic placement resulting presumably because Belokobylskij and Tobias (1986) had (incorrectly)

synonymised *Pseudavga* Tobias, 1964 (type species *P. flavicoxa* Tobias, 1964) with *Noserus*. This incorrect generic synonymy caused identification problems: the genus *Noserus* Foerster, 1863 (not 1862—see Foley et al. 2003) has been interpreted in various ways in the literature, but its type species *Noserus facialis* Foerster, 1863 was redescribed and figured by Whitfield and van Achterberg (1987) and clearly bore no relation to the reared British specimens, although *Noserus facialis* has been recorded from *Bucculatrix ulmella* (Tobias 1976, Belokobylskij and Tobias 1986, Belokobylskij 1998—the last two probably merely a reiteration of the first). However, when rearing records appear to have been transcribed from one work to another several times without clarification or further detail it is difficult to treat them with confidence, especially when the application of names to the parasitoid(s) has been inconsistent over that time. Thus the reliability of the parasitoid determination for this host record is possibly in doubt because Belokobylskij and Tobias (1986) and Belokobylskij (1998) incorrectly regarded *Pseudavga* as a synonym of *Noserus*, and this might conceivably underlie the citation of *B. ulmella* as host of both *flavicoxa* and *facialis* (which seems inherently unlikely to be the case) by Belokobylskij (1998), who keys *flavicoxa*, *facialis* (with the synonym *brevicauda*, but see below) and two Eastern Palaearctic species, *occipitalis* Belokobylskij, 1986 and *olgensis* Belokobylskij, 1994, all as species of *Noserus* (regarding both *Pachystigmus* and *Pseudavga* as synonyms). It was in a footnote that Belokobylskij and Tobias (1986) first stated that *Pachystigmus* Hellén, 1927 (type species *Pachystigmus nitidulus* Hellén, 1927, described from a single male) was a synonym of *Noserus*, and Whitfield and van Achterberg (1987) formalised the latter synonymy. Foley et al. (2003) showed that *Noserus* Foerster, 1863 (not 1862) is a junior homonym of *Noserus* LeConte, 1862, which is applied in Coleoptera, with the result that the name *Pachystigmus* has been resurrected and used subsequently (e.g. in *Fauna Europaea*).

In their attempt to clarify the application of the generic names *Cantharoctonus*, *Noserus* (now *Pachystigmus*, which has a different type species) and *Pseudavga*, Whitfield and van Achterberg (1987) stated that the type species of *Noserus*, *Pachystigmus*, *Pseudavga* and *Rhysipolis* had all been seen by van Achterberg. However, the paper then went on to diagnose and figure “*Pseudavga*” by reference not to the type species *flavicoxa* Tobias (Tobias 1964a), but to another nominal species that was at that time placed in *Pseudavga* (but incorrectly so), *Oncophanes brevicauda* Tobias, 1964, a nominal species (Tobias 1964b) now regarded as belonging in *Pachystigmus* and therefore congeneric with the nominal *Noserus facialis* (the proposed synonymy of *brevicauda* with *facialis* by Belokobylskij and Tobias (1986) has not been followed or accepted by van Achterberg (pers. comm.), and consequently both are listed as valid species of *Pachystigmus* in *Fauna Europaea*). This error in the recognition and diagnosis of *Pseudavga* was another major impediment to correctly identifying the reared British specimens as *Pseudavga flavicoxa*.

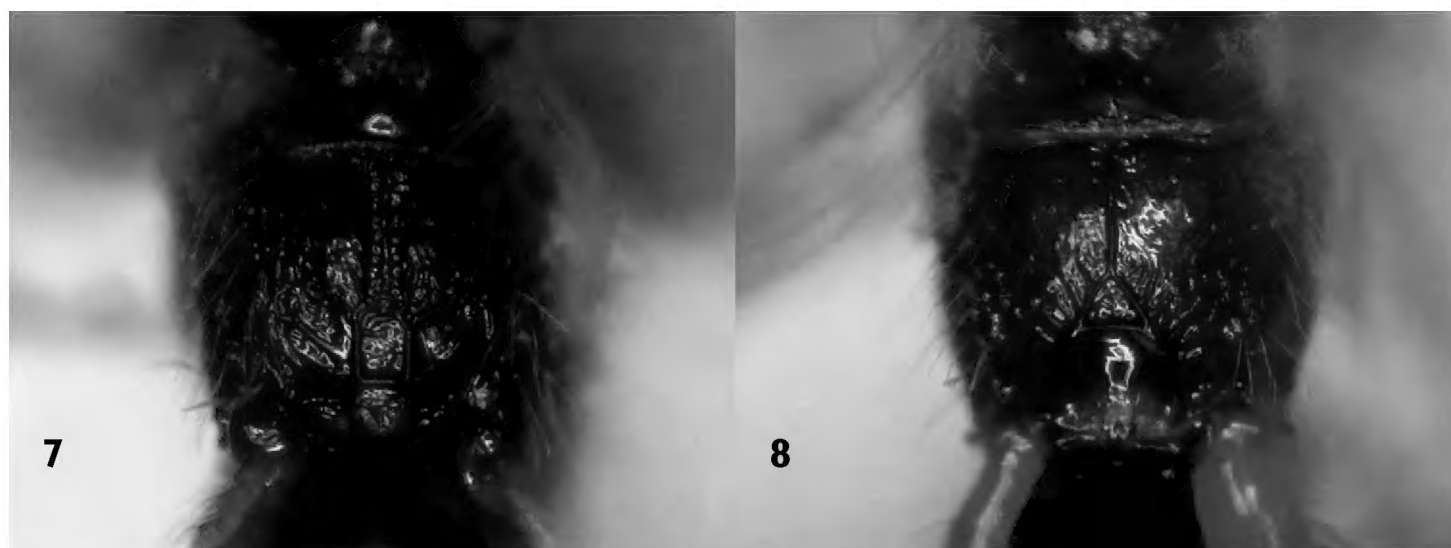
Generic placement

In *Fauna Europaea*, *flavicoxa* is listed as a species of *Rhysipolis* Foerster, although no formal synonymy of *Pseudavga* with *Rhysipolis* has been proposed. The propodeum is broadly similar in the two genera, with a clear median carina anteriorly, and with an areola and a

petiolar area more or less defined medioposteriorly. In *Rhysipolis* there is a wide divergence in the shape and relative sizes of the two latter areas: for example, in the type species *R. meditator* (Haliday) (Figure 7) the areola is moderately large, narrow, parallel-sided posteriorly with the short converging anterior sides to complete the pentagon being all but obscured in general rugosity, and the area petiolaris is almost unnoticeably small; while in *R. decorator* (Haliday) (Figure 8) the areola is very small, more or less reduced to a triangle, and the area petiolaris is by comparison massive. The propodeum of *P. flavicoxa* (Figure 2), with its relatively large pentagonal areola and small area petiolaris, sits fairly comfortably within these wide limits, closest to *R. meditator*, and it is presumably largely on account of the similar propodeum (in particular its anterior median carina) that van Achterberg placed *flavicoxa* in *Rhysipolis* in *Fauna Europaea*. However, *Pseudavga* has a significantly larger and wider areola and, unlike the situation in most *Rhysipolis* species, this has strong costulae. *Pseudavga* also differs from *Rhysipolis* in having a weak but distinct pronope (Figure 3) and in its legs bearing numerous long upstanding setae; furthermore, the spiracle of the second metasomal tergite is more deeply into the epipleuron (laterotergite) than in *Rhysipolis*. Perhaps even more obviously, *Rhysipolis* species have a longer ovipositor, commensurate with parasitizing hosts that are concealed in leaf mines and folds (Shaw 1983), whereas the short ovipositor of *Pseudavga* (Figure 1) is compatible with parasitism of fully exposed hosts (as reported here). Although the circumstantial evidence is that *Pseudavga* may have developmental biology similar to, or possibly identical with, that of *Rhysipolis*, these morphological differences justify its recognition as a genus distinct from *Rhysipolis*.

Sergey A. Belokobylskij (pers. comm.) has agreed with the present conclusion that *Pseudavga* is a genus distinct from *Pachystigmus*, regarding the reduced prepectal carina in *Pseudavga*, which is present only laterally [but variable; in some British specimens more extensive], as the most important difference. We have not seen the type of *Pachystigmus nitidulus* and consequently can offer no further opinion, but the original description (Hellén 1927) makes it clear that it is substantially different from *Pseudavga flavicoxa*, for example in the swollen male pterostigma of *nitidulus* (although this may not be a consistent generic character for *Pachystigmus*), and the figures given by Whitfield and van Achterberg (1987) of two further *Pachystigmus* species (*facialis* (as *Noserus*) and *brevicauda* (as *Pseudavga*)) also appear profoundly dissimilar.

However, whether or not *Pseudavga* should be retained as a genus distinct from the New World genus *Cantharoctonus* seems more doubtful, although in *Cantharoctonus* (to judge from the four undetermined N. American specimens in NMS) the complete prepectal carina appears to be much stronger than in *Pseudavga flavicoxa*, in which it is only weakly present. Whitfield and van Achterberg (1987) did not note similarities, but this must have been only because they misinterpreted *Pseudavga*, as in fact the two genera are in many respects extremely similar and both are parasitoids of *Bucculatrix*. Whitfield and van Achterberg (1987: Fig. 45) also seem to have misinterpreted the disposition of the hypostomal and occipital carinae in *Cantharoctonus*, in which (as in *Pseudavga*) in reality the carinae fail to meet, though converging towards the mandibular base, as the former peters out just before the mandible rather than, as Whitfield and van Achterberg (1987) state and figure, meeting well before the base of the mandible.



Figures 7, 8. *Rhysipolis* species, propodeum. **7** *R. meditator* **8** *R. decorator*.

(In fact it is apparent from detached heads of *Pseudavga flavicoxa* that the lower part of the hypostomal carina is not only extremely weak but also dissociates into a series of diverging ridges, the uppermost of which does more or less run into (or gives out just before) the very strong occipital carina before the mandibular base, but the lower and stronger of which runs on to the level of the mandible without meeting the occipital carina.) As well as an almost indistinguishable general facies, the two nominal genera also share the general arrangement of carinae on the propodeum (*Cantharoctonus*: Figs 8 and 47 in Whitfield and van Achterberg 1987), and the position (in the epipleuron) of the spiracle of the second metasomal tergite. One of the particular features of *Cantharoctonus* is a transverse and more or less crenulate groove across the extreme anterior edge of the propodeum, and in specimens in which this is well developed it is indeed quite striking. However, it seems to be rather variable in *Cantharoctonus*, and is to at least some extent discernible, if weak, on all the material of *Pseudavga* detailed in this paper. While a rather weak pronope is present in *Pseudavga flavicoxa* (Figure 3) it is stated to be absent in *Cantharoctonus* (Whitfield and van Achterberg 1987), but this may not have much significance (the dorsum of the pronotum is visible in only one of the specimens of *Cantharoctonus* in NMS). The legs of both genera bear long rather upright setae; somewhat less pronounced in *Pseudavga* (in which the setae on the hind tibia are almost as decumbent as in *Rhysipolis meditator*, the type species of *Rhysipolis*, unlike the specimens of *Cantharoctonus* seen). Whether the similarities between the two nominal genera are of greater significance than their differences might best be considered in the course of a thorough review of generic relationships in Rhysipolinae as a whole, as certainly seems to be needed.

Variation

Taken together, the available material of *Pseudavga* in NMS is very variable (e.g. in respect of colour, position of the radius on the pterostigma, shape and sculpture of the first metasomal tergite, detail of carination and sculpture of the propodeum, lengths of

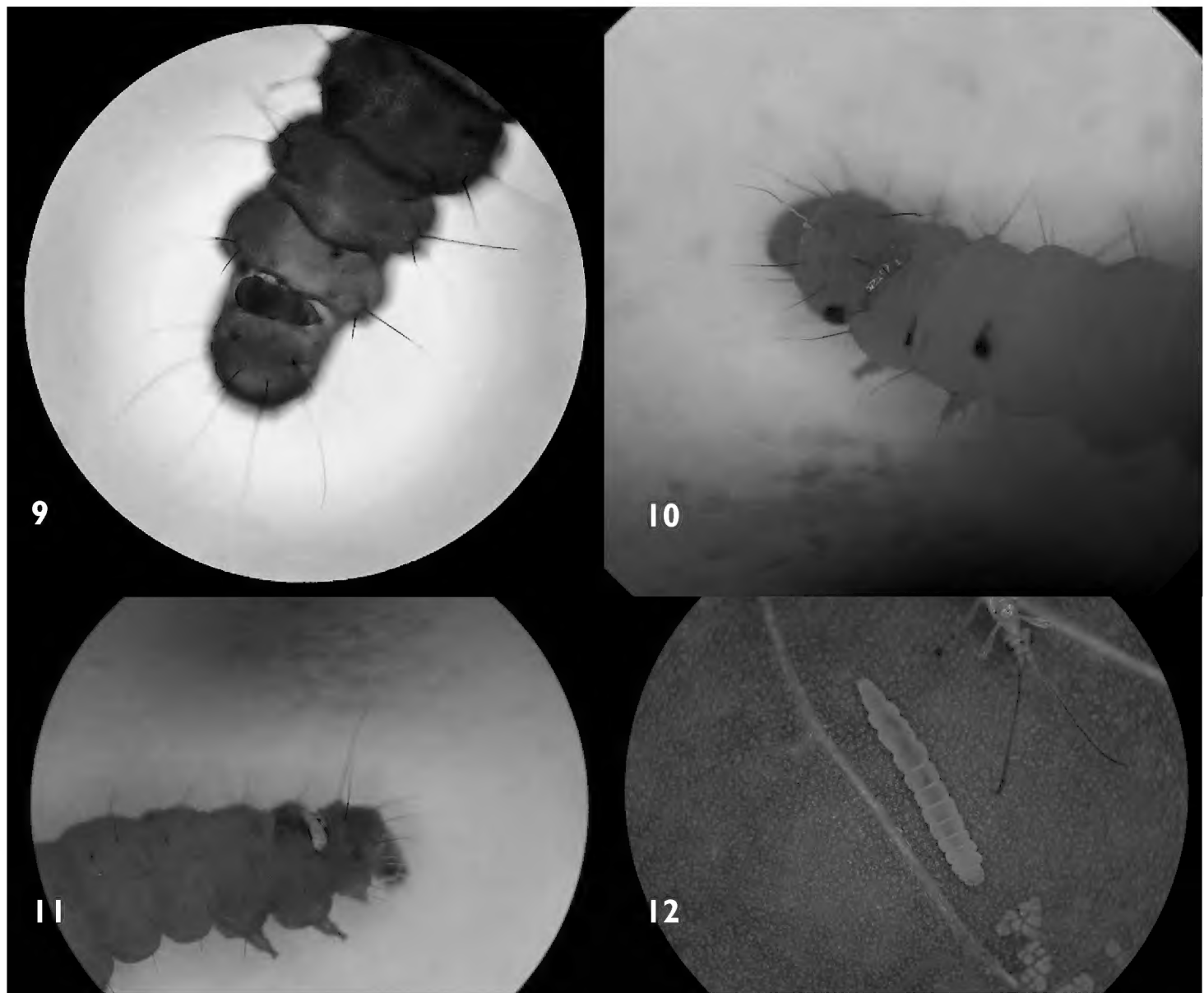
antennal segments and perhaps ovipositor sheath) and may represent more than one (possibly up to three) species. However, even though from a single population, there is enough variation in the British material (which must surely belong to only one species) to lead us to conclude that there is insufficient material at hand to assess possible species limits in the wider material in NMS, so provisionally we regard it as all belonging to a single variable species, *P. flavicoxa*.

Biological observations

The host of the British specimens, *Bucculatrix thoracella*, has greatly increased its range and abundance in Britain over the past 40 years, probably both through broadening its foodplant tolerance from *Tilia cordata*, a native but local and restricted woodland tree, to include the widely planted *Tilia × vulgaris*, and by becoming thoroughly plurivoltine (Emmet 1984). Thus from formerly being a local, uncommon and apparently univoltine denizen of mainly SW England, it is today widespread and common, especially in suburban environments where *Tilia × vulgaris* is frequently planted, over most of mainland Britain (including Edinburgh, where it is profoundly plurivoltine). After a brief period as a leaf miner, the larva of *B. thoracella* feeds on the parenchyma of *Tilia* leaves from the leaf underside, leaving a windowed pattern of damage visible from the upperside. To accomplish its moults, the larva constructs a temporary small and dense silken shelter, in which ecdysis occurs. When fully fed, the larva descends from the leaf on a silken thread, and spins its characteristic ribbed cocoon upon landfall.

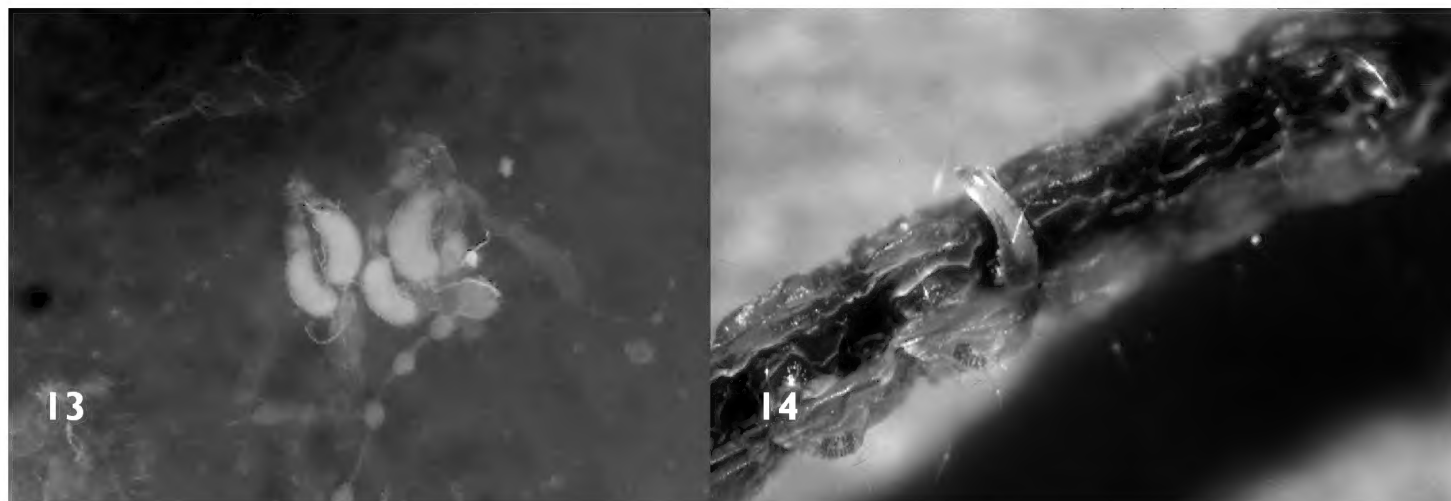
One of the descending *B. thoracella* larvae intercepted by IS on 2.x.2014 was being grappled by a small orange insect which (although it escaped) was almost certainly *P. flavicoxa*, and inspection of some other descending larvae revealed the presence of single eggs, 0.2 mm long and in each case (7 observations) transversely placed (sub) dorsally along the intersegmental membrane behind the first thoracic segment (Figures 9–11; from alcohol preserved specimens, 10–11 then air dried). The egg is rounded at both ends; the small dark point visible at the narrow (presumably caudal) end in Figure 9 is part of the host.

In Edinburgh, indoors at room temperature (18–22 °C), 1–2 mid-final instar host larvae were kept, on strips of *Tilia × vulgaris* leaf, in 2.5 × 7.5 cm corked glass tubes with a single (probably mated) female *P. flavicoxa* (6 replicates), with diluted honey smeared on the glass, from 13.x.2014 (after 3 days of feeding in the absence of hosts) until the females died (the last one on 25.x.2014). At times, hosts in moulting cocoons were also added. The hosts were inspected twice daily, and replaced as they formed cocoons; all cocoons were opened and the larvae within also inspected. No ovipositions resulted, and indeed (including during the initial period of inspection afforded to each female being newly introduced to hosts) no interest whatsoever in the hosts or their traces was observed (Figure 12). Most deaths of *P. flavicoxa* resulted from being gummed up in the traces of honey provided as food, and/or other



Figures 9–12. *Pseudavga flavicoxa* with final instar larval host *Bucculatrix thoracella*. **9–11** egg on intersegmental membrane behind prothorax of host **12** adult female parasitoid ignoring host.

fluid that appeared in the tube, and three adults suffering this fate were dissected (8, 9 and 12 days after 10.x.2014, when they had started to feed on dilute honey). The dissections hardly differed, each showing a single egg nearing maturity in each of the two ovarioles of the paired ovaries (i.e. 4 eggs in advanced ovigenesis, Figure 13), but with little sign that other eggs would follow. No egg had entered the oviduct per se, and it was unclear whether they were ready for oviposition or, conceivably, being resorbed. It does, however, seem certain that if eggs were going to be ready for oviposition from these females in October 2014, the period from 10.x.14 to (maximally) 25.x.2014, during which they had been warm, fed ad libitum, and given access to hosts, was long enough for them to have become so. Thus it was surprising that no ovipositions were obtained, especially as the adult female parasitoids showed no sign of behaviour suggesting that they might overwinter as adults (it has not, however, escaped notice that none of the adults of *Pseudavga* seen has unequivocally overwintered in a host cocoon).



Figures 13, 14. **13** *Pseudavga flavicoxa*, partial dissection of 12 day old female showing one almost mature egg in each of four ovarioles **14** *Rhysipolis decorator*, egg artificially partly detached from freeze-killed and stretched larva of *Caloptilia* sp.

Comparison with the biology of *Rhysipolis*

Although the act of oviposition per se has not been seen in either *Rhysipolis* or *Pseudavga*, there are some comparisons that can be drawn simply from observation of the eggs. In *Rhysipolis* the egg is similarly placed transversely across a host intersegmental membrane, though with much greater flexibility as to the segments concerned (Shaw 1983, reporting on three studied species), but the egg is much slenderer than that of *Pseudavga* (compare Figures 9 and 14). The eggs of *Rhysipolis* spp. presumably have to travel down the (relatively longer) ovipositor shaft because the host is concealed beneath plant tissue, and are consequently relatively slender; some flexibility regarding exact placement is likely also to be a consequence of host concealment. But the apparently more exact placement, and especially the less elongate egg shape, in *Pseudavga* raises the question of how, or whether at all, the ovipositor might be involved in egg placement. In particular, Shaw and Wahl (2014) have drawn attention to the possible universality of the egg (or at any rate the bulk of the egg) not travelling down the ovipositor shaft in all arthropod-consuming apocritan Hymenoptera whose larvae feed from an external position (the relevant ectoparasitoids and all carnivorous Aculeata) in which the female is able to make direct bodily contact with the host or prey at the time of oviposition. For this reason, microscopic observation of the moment of oviposition by *Pseudavga* would be of considerable interest.

Studied *Rhysipolis* species (Shaw 1983) employ a venom which, in addition to causing temporary paralysis aiding host-handling by the parasitoid, switches the host to a prepupal state of arrested development at the end of the instar attacked, precociously if the host is in its penultimate instar at the time of attack. In some cases, therefore, a given *Rhysipolis* species may develop on a nominally penultimate host. Although we have not seen suggestively undersized cocoons of the host (which, however, are uncommonly seen in the hosts of wild *Rhysipolis* populations), it would be of interest to know whether or not such a venom is employed by *Pseudavga*, and the unexplained failure to obtain attacks on the host in the autumn of 2014 was extremely disappointing.

Acknowledgements

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